

cludenti. *Tentacula* nulla. *Branchiæ* styliformes dorsi lateribus utrinque affixæ. *Anus* subposticus in medio dorso. *Aper-tura sexualis* pone caput in latere dextro.

Species unica *A. modesta**, Lovèn.

Hab. in limo, locis maritimis parum profundis.

II.—*Contributions to the Physiology of Fecundation in Plants.*
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[With a Plate.]

ALTHOUGH many interesting observations respecting fecundation in plants were contributed by the older botanists, it is chiefly to observers of the present century that we owe the facts now known respecting the structure of the ovule, its development previous to, and further progress after impregnation. The contributions of Brown, Amici, Brongniart, Mirbel and others to this department are invaluable, and when Schleiden in 1837 announced the "grand doctrine" as it has been called, that the extremity of the pollen-tube reaches the embryo-sac, indents it, carries it before it, and is itself then actually converted into the embryo, physiologists who formerly had written on this subject were stimulated to repeat their inquiries, new observers also entered the field, and the rash generalization of the observer alluded to has actually been the means of furnishing important additions to our knowledge of this most interesting branch of vegetable physiology. It can scarcely be doubted that much still remains to be known respecting this subject, and judging from the history of its progress, an accurate and complete acquaintance with it can only be arrived at by degrees and by the efforts of different observers. The quaint remarks of Nehemiah Grew, in his 'Anatomy of Plants,' appear to be so applicable to this matter, that no apology need be made for quoting them; he says, "That nothing hereof remaineth further to be known is a thought not well calculated. For if we consider how long and gradual a journey the knowledge of nature is, and how short a time we have to proceed therein; as on the one hand we shall conclude it our ease and profit to see how far others have gone before us, so shall we beware on the other, that we conceive not unduly of nature, whilst

* Though Lovèn's specific name, *modestus*, was evidently given to contrast with *ornatus*, the name of Ehrenberg's species, I have nevertheless abstained from changing it, though the congeneric relationship with *Stiliger* has been broken, and the name been consequently deprived of its original significance.

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we have a just value for those who were but her disciples and instructed by her. Their time and abilities both being short to her; which, as she was first designed by Divine Wisdom, so may her vast dimensions best be adjudged of in being compared therewith. It will therefore be our prudence not to insist upon the invidious question, which of her scholars have taken the fairest measure of her; but to be well satisfied, that as yet she hath not been circumscribed by any. Nor doth it more behove us to consider how much of the nature of vegetation may lie before us yet unknown, than to believe a great part thereof to be knowable. Not concluding from the acknowledged, much less supposed unsuccessfulness of any man's undertakings, but from what may be accounted possible as to the nature of things themselves."

On the Ovule of Narthecium ossifragum.

It is unnecessary to give any minute account of the ovarium in this plant; suffice it to say, that about the time of impregnation, in general form it resembles a Florence flask, the stigma is perforated, a canal traverses the style and appears to communicate with each cell of the ovary. Some authors seem to have misunderstood the structure and mode of attachment of the ovules: thus Endlicher, in his 'Genera Plantarum,' says, "Ovula e funiculis longis erecta;" and again, "Semina plurima, longe filiformia, funiculo crassiusculo elongato." In Sir W. J. Hooker's 'British Flora,' the seeds are described as having "a very long *arillus* forming an appendage to each extremity." The ovules have clearly no attaching cord; the outer membrane, of a lax cellular texture, is very greatly produced beyond the secundine and nucleus; the point of attachment to the placenta is by the edge of the exostome, from which, in consequence of the excessive development of the primine, there is a canal of some length leading to the foramen of the secundine and to the nucleus. In only one instance have I seen a distinct funiculus as is represented at fig. 4, Plate I., the usual mode of attachment being that which has now been described and is illustrated by fig. 1. This highly-developed primine has been mistaken for an *arillus*, from which however it is very different—at least if we follow the usual acceptance of the term.

While engaged in examining the ovules of *Narthecium* shortly after the bursting of the anthers, I found numerous transparent slender tubes on the surface of the placenta, and on careful examination was able to trace them to the mouths of ovules. I concluded at first that they were pollen-tubes, and proceeded to examine their connexion with the ovules. On dissecting off the primine, which is not a very difficult operation owing to its loose

adhesion to the other coats, I found the tubes to enter the mouth of the secundine, but after repeated observations was unable to detect any such connexion as that described by Meyen to occur between the end of the pollen-tube and the embryo-sac in some species of *Mesembryanthemum*, &c.; instead of which, the tube and the apex of the nucleus (as at present I suppose it to be) seemed perfectly continuous, the one being apparently a gradual prolongation of the other. This therefore induced me to examine the tubes in their whole course, and there were seen what I supposed to be the same tubes, terminating upwards in blind extremities. In one capsule the pollen grains which had fallen on the stigma were very few, while the ovules (in the same capsule) were most of them supplied with the organs described; I concluded, therefore, that they were not at all connected with the pollen. The position of the exostome in reference to the apex of the placenta (it is directed to the base of that organ, and consequently away from the descending pollen-tubes) appeared also to present an insurmountable objection, unless we suppose the pollen-tubes to be possessed of a remarkable instinct, which I presume physiologists would hesitate to ascribe to them. They must, in order to reach the nucleus after descending, find their way to the exostome and then ascend, passing along the canal leading to the endostome. The smallness of the aperture in the outer membrane and its irregular margin would render it difficult for a pollen-tube to hit upon it exactly, keeping out of view altogether its direction. On the outside of the tubes described, were numerous spherical molecules, some of which were in active motion, and occasionally a few similar particles were seen in their interior. I afterwards found that these molecules were abundant in the tissue of the placenta. The opinion first entertained about these organs (*ovule-tubes*), viz. that they had their origin from the pollen, was for these reasons abandoned. Supposing them to be prolongations of some part of the ovule itself, an objection having reference to the position of the exostome, and the passage of the tubes upward towards the apex of the placenta, might with great justice be urged; I found, however, that they in common have a great tendency to become tortuous and bent upon themselves: such a tube therefore, on issuing from the exostome, and on being bent from its original direction, would come in contact with the placenta, and might have its further course regulated by contact with that organ. Without however laying much stress upon this, or venturing to speculate more in the matter, it may be remarked that the mode of growth of the tube would assist materially in regulating its course, especially if its increase in length took place at

the extremity and not through its whole extent. The objections to the tubes being prolongations from the ovule will lose their force, when we call to mind the remarkable facts ascertained by the late Mr. Griffith respecting the ovule of *Santalum*. In this plant the nucleus is naked, primine and secundine being absent; at a certain stage "a tubular membrane protrudes from the centre of the apex of the nucleus, in which no opening can be detected previously. This tubular membrane passes down at first in the direction of the axis of the ovulum, but becomes immediately recurved, and passes up one side of the ovulum and in close apposition to the placenta;" again, "the tubes remain in apposition to the placenta, and continue to be simple, membranous, elongated, closed tubes." (Linn. Trans. vol. xviii. p. 60, &c.) This membranous tube Mr. Griffith believed to be the sac of the amnios, "which in ordinary structures lines the cavity formed in the nucleus at some period previous to fecundation, and which, at least in its earlier stages of development, is the only coat that is membranous." M. Ad. Brongniart many years ago announced the discovery in the interior of the nucleus of a special membranous tube often prolonged beyond the ovule, and which establishes a communication between the conducting tissue of the placenta and the point where the embryo is formed. This was observed in some *Cucurbitaceæ*, in several species of *Polygonum*, and other plants. The same structure had however been previously discovered by M. de St. Hilaire. These *ovule-tubes* are probably of more frequent occurrence than has been supposed: I have seen them in great abundance on the placenta of *Bartsia Odontites* and *Euphrasia officinalis*: I was unable to trace their origin from the pollen, but had no difficulty in seeing their connexion with the ovules, and their adhesion to or rather continuity with the apex of the nucleus. It was at first suspected that they were pollen-tubes; this idea was soon abandoned when they were found to terminate in blind extremities toward the upper part of the placenta. In young ovules they were seen protruding from the exostome in the form of minute transparent papillæ; in others further advanced their increase in length was very evident. Similar tubes were found in connexion with the ovules in *Parnassia palustris*. I believe them to be prolongations of the apex of the nucleus in *Narthecium*, *Bartsia* and *Euphrasia*.

In the 16th volume of the 'Transactions of the Linnæan Society,' Mr. Brown, in his essay on the Mode of Fecundation in the *Orchideæ*, has stated the existence of "mucous cords" or tubes on the placenta of several plants belonging to that family. In the first part of this essay Mr. Brown supposed that these tubes were actually derived from the pollen, but he had not been

able satisfactorily to trace them to the ovules. In an appendix, however, this opinion is essentially changed, and the direct origin of these tubes from pollen grains is doubted; it is also stated that in *Orchis Morio*, *Habenaria viridis* and *Ophrys apifera* they were traced into the apertures of the ovule. M. Schleiden spoke with greater confidence, and described the pollen-tube in the *Orchideæ* as entering the foramen of the ovule, its extremity becoming converted into the embryo; Meyen expressed himself to the same effect, and Link has represented this occurrence in *Gymnadenia conopsea*.

That "mucous tubes" are found in connexion with the ovules cannot be called in question; that these are pollen-tubes appears to be not yet satisfactorily proved.

Such tubes are abundant in *Habenaria viridis*, and from an examination of this plant I have reason to believe, but shall not at present positively assert, that the tubes are derived from the ovules themselves and not from the pollen.

The ovule in the *Orchideæ* is of exceedingly simple structure; a nucleus, at first partially, afterwards entirely covered by a single membrane, the two becoming ultimately so fused together that the testa appears composed of one layer only. Mr. Brown, in the essay already quoted, states that soon after this change a minute opake body makes its appearance about the middle of the cavity of the testa; he also traced a jointed thread from its apex nearly to the open end of the testa. This thread, with its dilated extremity, Meyen and Schleiden have mistaken for a pollen-tube. Mr. Brown very accurately describes this thread as consisting of a simple series of short cells, "the lowest cell being probably the original state of what afterwards becomes the embryo." I believe that a prolongation of the uppermost cell of this thread, beyond the opening of the testa, accounts for the presence of the mucous tubes so abundant upon the placenta. The appearances described can be readily seen in *Habenaria viridis*, and the simple cellular structure of the embryo, even when nearly mature, is evident in *Goodyera repens*. The jointed thread in *Habenaria viridis* is at first straight, and the cells composing it have a firm adhesion to each other; when the lowest cell (the embryo) has attained considerable size and is nearly mature, the cord which issues from the mouth of the ovule breaks off at some joint near this opening; the rupture is preceded by an evident change in the mutual position and connexion of the cells, the whole cord becomes tortuous, the points of adhesion of the cells diminish in extent, and the joints easily separate from each other. Even in seeds to all appearance fully ripe I have seen the thread broken off at the mouth of the testa, while the remaining cells were still

attached to the embryo. The ripe seed of this plant, as well as other *Orchideæ*, is quite destitute of vessels *; in *Narthecium* vessels do not appear until some time after fecundation.

It is exceedingly probable that the emission of such prolongations, *ovule-tubes* as they may be called, to meet the descending *pollen-tubes*, may be of frequent occurrence. It is possible that some of those cases in which pollen-tubes are described as having been seen entering the foramen of the ovule, may have been instances of such prolongations as exist in *Narthecium*.

Supposing it to be a settled point that contact of pollen-tubes with some part or other of the ovules is necessary to secure the full development of the embryo,—and some authors are of this opinion,—there seem many physical difficulties in the way of the pollen-tubes reaching their destination; these have reference to the length of the style, the nature of the tissue of which it consists, the form of the ovule, the position or direction of the exostome, the number of the ovules and other circumstances. Sure it is, that difficulties cannot stand before demonstration. True pollen-tubes have no doubt been in many instances traced into the tissue of the stigma and style, and in some cases to the placenta, and it may be, even to the ovule itself, but instances of this last are far from numerous. In order to secure the effect of the pollen upon the ovule, or at all events to diminish the chance of this action failing, it may not be unreasonable to expect that some such arrangement would be provided as that, the existence of which in *Narthecium* I have been attempting to prove. Observers so frequently meet evident instances of design in the structure of organs,—it may even be said of less importance than those under discussion,—that it is extremely probable the present may be a case in point.

It has been already remarked, that the number of the ovules presents a difficulty in the way of the contact of a pollen-tube with each; and where they are very numerous and arranged in regular series from the base to the apex of the placenta, it is very evident that those occupying the latter position stand a better chance of being fecundated than those toward the lower part. The emission of tubes from the ovules to meet the descending pollen-tubes would evidently diminish the chance of failure. In such cases it would be interesting to ascertain whether all are usually impregnated or what proportion of them only, and whether those taken from the upper part of a capsule contain a greater proportion of fecundated individuals than those from the lower part of the same.

* *Callitriche verna* presents an instance of non-vascularity in filaments and anthers.

The position of the exostome in reference to the direction from which the pollen-tubes come, presents also a difficulty: *Narthecium* is a remarkable instance, and many others must be familiar to those who have been accustomed to dissect ovaries and ovules.

In certain cases, some ovules, owing to the direction of the exostome, are more favourably placed for fecundation than others in the same capsule; for example, in certain species of *Spiræa*, *Æsculus* and others. There are instances in which only one ovule reaches maturity, the other or others in the same capsule being abortive: a question arises whether this has any connexion with the development or non-development of certain parts of the ovule, or to the obstacles presented to the action of the pollen; some remarks on this will be found in the essay of the late Mr. Griffith, in reference to *Santalum* and *Osyris*, whose embryology he has so admirably illustrated. The question respecting the particular part of the ovule which sends off a prolongation to meet the descending pollen-tubes may be left for future consideration; suffice it for the present to say that *ovule-tubes* do exist in several families; their presence has been shown in plants belonging to the *Cucurbitaceæ*, *Chenopodiaceæ*, *Polygonaceæ* and *Santalaceæ*, and to these may be added *Juncaceæ*, *Scrophularineæ* and *Parnassicæ*, probably also in *Orchideæ*. The mode of contact between *ovule-tubes* and *pollen-tubes*, and the subsequent changes, will also present an interesting field for investigation. The subject is one of considerable importance, and it is remarkable that in most physiological works, even the more recent, no allusion whatever is made to it, although Brongniart's observations were published many years ago. There is great reason to suspect that when transparent tubes have been seen attached to ovules, they have, without further examination, been set down as originating from the pollen.

EXPLANATION OF PLATE I.

- Fig. 1.* Fragment of placenta and two ovules of *Narthecium* some time previous to fecundation.
- Fig. 2.* Ovule from the same plant about the time of fecundation, showing *primine*, *secundine* and *nucleus* with its tube.
- Fig. 3.* *Secundine* and *nucleus* extracted from the *primine*. This figure must be considered more as a plan made out from several observations than an actual representation of the appearance seen in any one ovule.
- Fig. 4.* A solitary instance in which a distinct funiculus existed.
- Fig. 5.* Young embryo and its jointed thread from *Habenaria viridis*.
- Figs. 6 and 7.* The same at more advanced periods.